

## Respiration and Metabolism in Two Baleen Whale Calves

ERIC A. WAHRENBROCK, GARY F. MARUSCHAK, ROBERT ELSNER, and DAVID W. KENNEY

Eric A. Wahrenbrock and Gary F. Maruschak are members of the staff of the Anesthesia Laboratory of the School of Medicine, University of California, San Diego, La Jolla, CA 92037. Robert Elsner is a member of the staff of the Physiological Research Laboratory of Scripps Institution of Oceanography, University of California, San Diego, P.O. Box 109, La Jolla, CA 92037. David W. Kenney was formerly a member of the staff of Sea World, Inc., San Diego, Calif.; his present address is 14220 Poway Rd., Poway, CA 92064.

### ABSTRACT

*We performed respiratory and metabolic studies on two female gray whale calves. Although one died 2 months after capture, the other thrived during a year's captivity, permitting serial observations while growing, and weighed in excess of 6,350 kg when released. They appeared to be of normal size and weight compared to whales in the wild. Relative increases in body length and weight, lung volume, minute ventilation, and metabolic rate were similar to those in terrestrial mammals, as was the growth efficiency. Lung volume and metabolic rate could be predicted with only partial success from the relationships of those variables to body weight proposed by Tenney and Kleiber, perhaps due to immaturity in the whales.*

*Compared to terrestrial mammals, the ratio of tidal volume to resting lung volume in the whale was large, while the ratio of wasted ventilation to tidal volume was small. We measured respiratory excursions of arterial O<sub>2</sub> and CO<sub>2</sub> tensions of 36 and 16 mm Hg, respectively, consonant with the relationships between respiratory rate, lung volume, tidal volume, and metabolic rate.*

### INTRODUCTION

Although the physiology of toothed whales, particularly porpoises, has been studied at some length (Irving, Scholander, and Grinnell, 1941; Olsen, Elsner, Hale, and Kenney, 1969; Olsen, Hale, and Elsner, 1969; Scholander, 1940), the study of living baleen whales has been particularly elusive. The size and dietary habits of these large mammals present formidable obstacles to their maintenance in captivity, and these obstacles are compounded by ignorance of the whales' growth rate, dietary requirements, metabolism, and hematologic and cardiorespiratory physiology.

However, these and other aspects of the biology of baleen whales are, in many respects, unique among mammals; research would therefore be

doubly rewarding. This line of reasoning led to the capture and study of the two animals reported herein, and to this workshop.

We were naturally inclined toward studies of especial personal interest, and recognize their limited scope and serious omissions (cardiac output, for example). We are here reporting observations on growth, respiratory function, and metabolic rate; additional reports of detailed nutritional, metabolic, biochemical and hemotologic studies; inert and anesthetic gas uptake; and respiratory mechanics will follow.

### METHODS

The first gray whale calf (Gigi I) was captured in Scammon's Lagoon, Baja California, Mexico in February

1965 and brought to San Diego, where a number of respiratory and metabolic studies were performed. Although the whale at first seemed to thrive, it died of an uncontrollable infection about 2 months after it was captured.

The second calf, Gigi II, was captured in March 1971, again in Scammon's Lagoon, and was again kept in (increasingly larger) pools at an oceanarium in San Diego. Gigi II thrived indeed: gained in size, was weaned, was studied intensively, and was reluctantly (but inevitably) released almost exactly a year after her capture.

Two of the authors were members of each of the expeditions (DWK and RE on the first, and DWK and EAW on the second) and one of us (DWK) was responsible for the medical care of both animals while in captivity.

For most of the studies reported here, the water level in the tank was lowered so as to nearly immobilize the whale, leaving about 12 inches of dorsal body surface above the water level, and the blowhole barely awash. A few of the studies were performed with the whale completely stranded on the bottom of the empty tank.

The respiratory pattern in whales and other marine mammals consists of an expiration followed by an immediate inspiration, followed by an interrespiratory pause during which

the airway is closed. The duration of the pause in Gigi II was about 1 minute, and inspiration and expiration together required about 2 seconds. Two observations can be made from this respiratory pattern (commonly called "apneustic"): 1) a valve would be needed in order to separate inspiration from expiration, and 2) resting lung volume is different from that in terrestrial mammals, because in cetaceans it includes the tidal volume.

Accordingly, we fabricated nonbreathing valves: first of approximately 5 inches diameter, and later (for Gigi II) of 8 inch stovepipe (Figure 1), thus permitting us to collect uncontaminated exhaled gas. For Gigi I a large, calibrated, counterbalanced, bellows-type spirometer was used; and for Gigi II, expired gas was collected in 900 liter meteorological balloons. The volume of exhaled gas was then measured by emptying the balloons through a calibrated dry gas meter (Wright Spirometer or American Meter Co.)<sup>1</sup> at a constant, known flowrate. Aliquots of mixed expired gas from Gigi I were analyzed for O<sub>2</sub> and CO<sub>2</sub> with a Scholander apparatus, and for Gigi II with a modified Haldane apparatus (Lloyd-Gallenkamp), as were samples of end-tidal gas, obtained from a port just beyond the expiratory valve leaflet of the nonbreathing device.

Resting lung volume was measured in Gigi II by injecting 1.50 liters of pure helium into the inspiratory port of the nonbreathing valve during inspiration. The subsequent expiration was captured, and mixed expired gas analyzed for helium with a sensitive, calibrated katharometer (W. E. Collins).

Arterial blood was drawn from Gigi II by percutaneous puncture of the digital artery in a flipper with an 18 gauge 3 inch needle, and arterial placement ensured by observing pulsations of blood through the needle. Because of the configuration of the

arterial and venular system, it is possible that arterial blood was contaminated at times with venous blood. Some of the gas samples from Gigi II, and all of her blood samples, were analyzed for O<sub>2</sub> and CO<sub>2</sub> tensions ( $P_{O_2}$  and  $P_{CO_2}$ ) with a blood gas analyzer (Radiometer BMS-3), with which blood pH could also be determined.

From timed gas collections during which the number of breaths was also counted, respiratory rate, minute ventilation, tidal volume, oxygen consumption, and wasted ventilation (or "dead space" fraction,  $V_d/V_t$ ) could thus be determined by suitable analysis.

## RESULTS

In the first few weeks of captivity, each whale lost weight, but gained thereafter (Figure 2). The rate of gain during the first 8 months was about 200 kg/mo in Gigi II.<sup>2</sup> She was weaned at about 7 months of age, as are calves in the wild (Rice and Wolman, 1971). At age 10 months, she entered a very rapid growth phase during which her food intake increased from about 1,200 to about 1,800 pounds of squid/day, and her rate of gain in weight increased almost 5 fold, to 970 kg/mo or (for those of us who enjoy such reductions) approximately 3 pounds/hour. Each whale gained in length regularly: although Gigi I was smaller than Gigi II when captured, their increases in body size were similar (Figure 3). This suggests that the infection did not seriously impede her growth.

Respiratory rate ( $f$ ) was counted on many occasions; it varied with the whales' activity. It averaged 2/min for Gigi I at first, and increased to 4 or 5/min after age 2 months. However, this whale had atelectasis and pneumonia secondary to a harpoon wound,

<sup>2</sup> Both calves were first fed by gavage, and in both the liquid diet was gradually changed from mainly whipping cream to a mixture of ground squid, ground bonito, calcium caseinate, yeast, and corn oil. For Gigi II, the proportion of squid in the diet was gradually increased until the time of weaning.



Figure 1.—Nonbreathing valve for Gigi II, constructed of 8 inch stovepipe and containing one quarter inch neoprene foam rubber valve leaflets. Inspiration was from the side-arm, and the inspiratory valve leaf and its supporting ring were slanted so that closure was assisted by gravity.

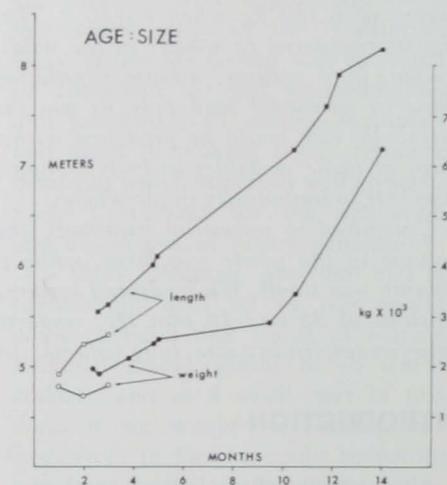


Figure 2.—The whale was weighed with an industrial heavy duty scale (Dynamometer) by lifting her from the water with a crane while supported on a canvas and pipe stretcher, and subtracting the tare weight. Body length was measured on a straight line from lips to notch in fluke. Data from Gigi I are represented by open circles and squares, and for Gigi II by solid symbols. Length in meters on left hand scale; weight in thousands of kilograms on right hand scale.

leaving the meaning of this observation somewhat uncertain. When Gigi II was motionless, or nearly so,  $f$  averaged 1/min, irrespective of age. Accordingly, tidal volume ( $V_t$ ) and minute ventilation were nearly equal (Figures 4, 5). Each value for  $V_t$  is an average of three or more measurements, as we observed that  $V_t$  varied

<sup>1</sup> Reference to name of firm does not imply endorsement by the National Marine Fisheries Services, NOAA.

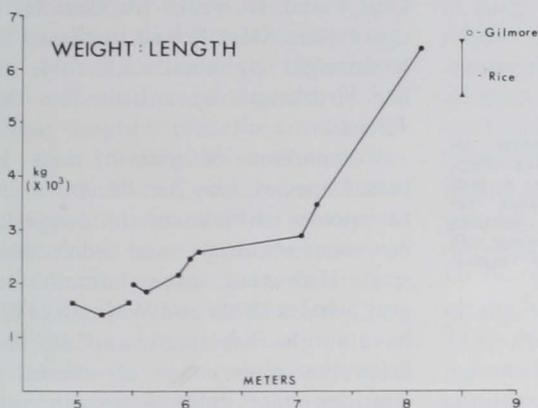


Figure 3.—Weight plotted as a function of length in the two gray whale calves. Data from Gigi I is represented by squares, and from Gigi II by circles. At the time of the rapid weight increase Gigi II was approximately 9.5 months old. Gilmore (1961) reported data from one calf which died after being stranded in San Francisco Bay. Data from Rice and Wolman (1971) represent north and southbound calves (lower and upper points respectively); the difference supports the hypothesis that gray whales fast during the southern migration.

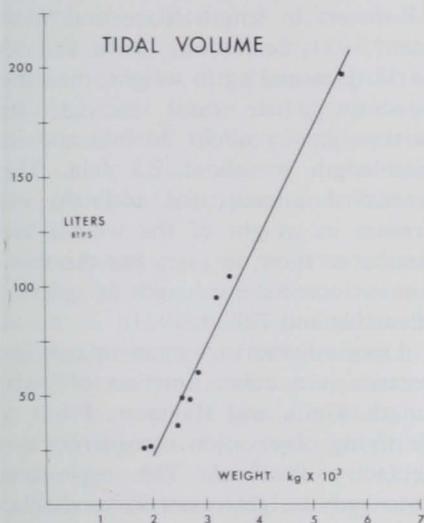


Figure 4.—Tidal volume ( $V_t$ ) in a gray whale calf during the first year of life. The regression equation for the line is:  $V_t = (47 \times \text{body weight in metric tons}) - 70$ . The correlation coefficient  $r = 0.99$ .

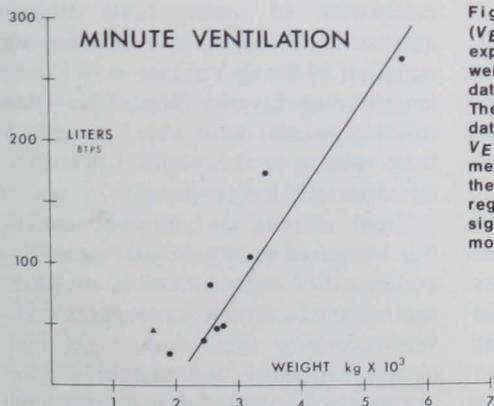


Figure 5.—Minute ventilation ( $V_E$ ) in two gray whale calves, expressed as a function of body weight. The triangle represents data from observations in Gigi I. The regression equation for the data from Gigi II (circles) is:  $V_E = (70 \times \text{body weight in metric tons}) - 117$ . Although the  $r = 0.94$  for this rectilinear regression, it is apparent that a sigmoid curve could be even more closely fitted to the data.

markedly from one breath to the next, sometimes by 50 percent.

Resting lung volume, (Figure 6) necessarily varied from breath to breath also, and in addition, the measurement was technically difficult because of the difference between inspired and expired  $V_t$ . Nevertheless, five measurements were felt to be adequate. Two measurements were made at weight = 6,150 kg, one when awash and one when stranded on the bottom of the completely drained tank. Lung volume was reduced by about 20 percent by stranding, although that value was determined only once.

From time collections of mixed expired gas, oxygen consumption was computed (Figure 7). The composition of end tidal gas from Gigi II was determined on several occasions, and did not vary systematically with age. End tidal  $P_{O_2}$  varied from 54

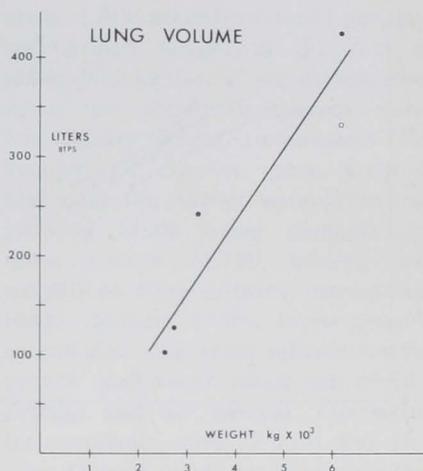


Figure 6.—Resting lung volume in a gray whale calf (Gigi II), expressed as a function of body weight. Resting lung volume includes tidal volume, and is the volume of gas in the lungs during the intervals between breaths. The equation for the line is: lung volume =  $(70 \times \text{body weight in metric tons}) - 44$ ; for which  $r = 0.94$ .

Table 1.—Arterial blood gas tensions and pH, drawn at random during the respiratory cycle.

Item	Age, months		
	2.5	3.0	10
PaO <sub>2</sub> , mm Hg	55	62	60
PaCO <sub>2</sub> , mm Hg	56	69	41
pH	7.23	7.32	7.35

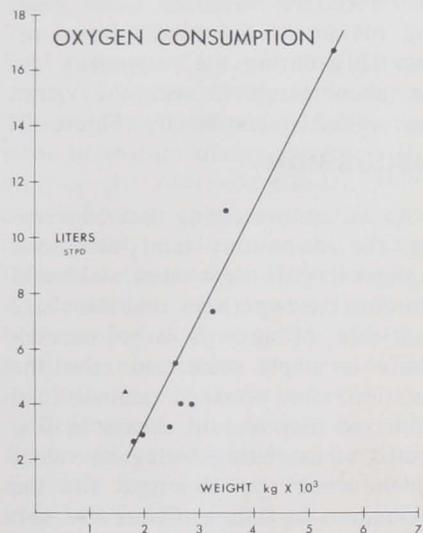


Figure 7.—Oxygen consumption in liters/min ( $V_{O_2}$ ) in two gray whale calves, expressed as a function of body weight. The triangle represents data from observations in Gigi I. The regression equation for the data from Gigi II (circles) is:  $V_{O_2} = (4.1 \times \text{body weight in metric tons}) - 5.7$ ; for which  $r = 0.96$ .

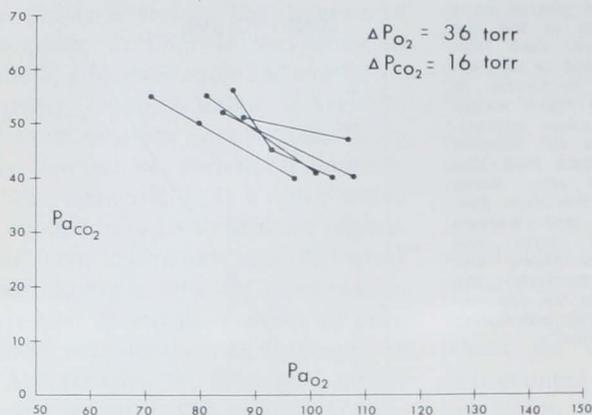


Figure 8.—Arterial  $O_2$  and  $CO_2$  tensions ( $Pa_{O_2}$  and  $Pa_{CO_2}$ ) in a gray whale calf, from sequential blood samples drawn about every 15 secs during five respiratory cycles.

to 85 mm Hg, and the corresponding  $P_{CO_2}$  varied from 75 to 54 mm Hg. We computed wasted ventilation from the difference between end tidal and mixed expired  $P_{CO_2}$ . It equalled 13.0 percent of  $V_t$  at age 3 months and 13.5 percent at age 13 months.

Arterial  $P_{O_2}$ ,  $P_{CO_2}$ , and pH were measured on three occasions in samples drawn at random during the respiratory cycle. (Table 1). Those values also varied considerably: the differences between arterial and alveolar  $P_{O_2}$  and  $P_{CO_2}$  were difficult to interpret, and were sometimes negative. Therefore, we measured blood gases and pH in arterial blood drawn sequentially during the respiratory cycle (about every 15 sec): the values then varied systematically (Figure 8).

## DISCUSSION

As we are presenting data concerning the respiratory and metabolic changes in growing whales, we should examine the hypothesis that their size and rate of growth were normal. There is ample reason to raise the question, for confined animals fed contrived diets should always be suspected of exhibiting biological values which would be abnormal for the population in nature. There are two methods of examining this question: to make comparisons with other gray whales; and to look for internal evidence of abnormal growth and development.

Data from Gilmore (1961) and

Rice and Wolman (1971) comprise the first method, for they have examined gray whale calves similar in age and size to Gigi II. Her weight and length at the time of release compare favorably to the other data on calves thought to be yearlings (Figure 3). As gray whales in the wild are thought to fast during the southern migration (Rice and Wolman, 1971), the observation that Gigi II was slightly heavy for her length should be interpreted with caution.

The internal evidence relating to the question consists of the observation that Gigi II sustained an increase in body length which preceded any considerable growth in body weight, mitigating against an argument that she was grossly overweight or overfed, and which is consistent with the pattern of early growth in other mammals (i.e., exponential for weight and linear for length) (Christian, 1972; Carlander and Ricker, 1962; Brody, 1964).

Although there is some disagreement (Gilmore, 1961, and pers. comm.), newborn gray whales are estimated to be 4.9 meters in length at birth (Rice and Wolman, 1971). Their birthweight is less certain, although Rice proposes the weight of the products of conception at term to be between 1,000 and 2,000 kg. Our estimates of the birthweight of the two whales at about 1,500 kg, and the birthlength at just under 5 meters are therefore consistent, and permit extrapolation of their ages at capture to 4 weeks for

Gigi I and 10 weeks for Gigi II. At age 1 year, Gigi II had increased her birthweight by about 3.5 fold, and her birthlength by a little less than 1.5 fold.

Comparison of growth rates between species may be deceptive due to species differences in longevity, newborn maturity, and adult body size. However, since humans and gray whales (Rice and Wolman, 1971) have similar life spans, and are both large mammals, it is of interest to consider their relative growth rates in body weight, respiration, and metabolism.

If mature female gray whales are 13 meters in length (Rice and Wolman, 1971; Scammon, 1874), and 30 to 35 thousand kg in weight, then the newborn whale must increase its birthweight by about 20 fold and its birthlength by about 2.5 fold. The fractional annual and ultimate increases in weight of the whales are similar to those in man, but the fractional increase in length is greater (Benedict and Talbot, 1921).

Lung volume in human infants increases as a cubic function of body length (Cook and Hamann, 1961), a satisfying observation considering the geometry involved. The regression onto body weight is not very reliable; the regression onto length is approximately: Total Lung Capacity (liters) = body length (meters) cubed. Although we have insufficient data for the whale to make firm conclusions (and have arbitrarily linearized the data against body weight in Figure 6), calculation of resting lung volume against body length suggests that an equation of Lung Volume =  $0.62 \times \text{length}^3$  also fits the data. This relationship seems reasonable, as resting lung volume in the whale is probably less than total lung capacity.

Tidal volume and minute ventilation increased during the year's growth, and as a first approximation, we have again linearized the data (Figures 4,5). We recognize that changes in respiratory function and metabolic rate are probably not rectilinear functions

of body weight, but we also recognize that the data available to us represent only a small portion of the full curves. Tidal volume increased about 8 fold as body weight tripled: the corresponding value for minute ventilation was 10 or 12 fold. Comparison of this growth rate with that of terrestrial mammals is awkward, because of marked changes in their respiratory rate during growth (Watson and Lowrey, 1962), while respiratory rate in the whale was constant. In terrestrial mammals, tidal volume changes as a function of lung volume (which in turn varies as a cubic function of length), while minute ventilation changes as a function of metabolic rate (Tenney and Kemmers, 1963); a more complex function of growth, which is not linear on any convenient parameter of body size because of growth spurts during early and late childhood (Benedict and Talbot, 1921).

The increase in the metabolic rate of Gigi II corresponded to the increase in her ventilation, and for a tripling of weight, increased about 10 fold. This increase is of the same order as the increase in human metabolic rate during the first year (about 8 fold) (Benedict and Talbot, 1921), and is consistent with our general impression that growth in the whale, whether of body weight, lung volume, or metabolic rate, proceeded in parallel with, or only slightly more rapidly than, human growth.

Observation of animals at the extremes of body size invites interspecies comparisons of biological phenomena. The existing data for two such correlations; of lung volume with body size (Tenney and Remmers, 1963), and of metabolic rate with body size (Kleiber, 1961), are particularly well organized. Tenney has shown that lung volume is closely related to body mass (over a range of body mass of 5 orders of magnitude) by the equation:  $\log \text{lung vol} = 1.02 \log \text{body weight} - 1.25$ , with volume in liters and weight in kg. This yields a predicted lung volume

in Gigi II of 410 liters at 6,150 kg, which corresponds closely to our measurement of 428 liters, but which diverges widely from values obtained early in her growth. Tenney measured total lung capacity (TLC) of excised lungs, and we measured resting lung volume: this ordinarily considerable difference is fortuitously minimized by the fact that resting lung volume in the whale is a larger fraction of TLC than is the case for terrestrial mammals. This measurement permits considerable extension of Tenney's data, for his largest animal, also a cetacean, weighed only 1,750 kg.

Kleiber studied the metabolic rates of animals also differing in body size by about 5 orders of magnitude, and concluded that metabolic rate was best related to the 0.75 power of weight, by the equation:  $\log M = 1.83 + (0.756 \log W) \pm 0.05$ , with  $M$  in kcal/day and  $W$  in kg. Using the conversion factor of 4.8 kcal = 1 liter of  $O_2$ , the whales' metabolic rates compare favorably with that regression line up to a body weight of 3,000 kg, but diverge significantly thereafter. The last metabolic rate measured was 16.8 l/min, while the calculated value from Kleiber's equation is 6.8 l/min. It is notable that metabolism in Gigi II, Benedict's elephant, and Irving's whale all differ from Kleiber's prediction, thereby raising the question of whether large mammals do indeed follow the 0.75 power rule. However, the value for the 70,000 kg fin whale was extrapolated from a measurement in a porpoise (Irving, Scholander, and Grinnell, 1941), and neither the elephant nor our whales were studied under conditions meeting Kleiber's criteria of ambient temperature neutrality, adulthood, and basal postabsorptive state. The resulting errors would be in the direction of the observed differences. Divergence from the 0.75 power rule may also be seen in growing cattle, horses, children, and rodents (Brody, 1964).

During the phase of rapid weight gain, Gigi II ate from about 1,200 to

about 1,800 pounds of squid per day, and gained weight at the rate of about 980 kg/mo. If we assume that squid are about 80 percent water and the dry weight is equivalent to 5 kcal/gm (R. Lasker, pers. comm.), and make the further assumption that growing whale tissue contains the same energy (1,720 kcal/kg wet weight) as other growing mammalian tissue (Mayer, 1949), it is possible to calculate the gross efficiencies for growth of a baleen whale calf of 10.3 percent and 6.9 percent. Correcting for metabolic rates of 11.0 and 16.8 liters  $O_2$ /min yields net efficiencies for growth of 12.0 percent and 8.0 percent (Brody, 1964). In general, growth efficiency is independent of body size (Kleiber, 1947), but is a diminishing function of metabolic age: the calculated values are within the expected range for terrestrial mammals beyond the first doubling of body weight (Brody, 1964).

Tidal volume equalled about 50 percent of resting lung volume, irrespective of age or size. This is a smaller ratio than that reported for other diving mammals (Irving et al., 1941; Olsen et al., 1969; Scholander, 1940), although they were mature. The ratio of wasted ventilation to tidal volume ( $V_d/V_t$ ) in Gigi II was about 13 percent, irrespective of age. This value is consistent with observations in mature diving mammals (Irving et al., 1941; Scholander, 1940, and Kooyman, pers. comm.), and is considerably smaller than the ratio in terrestrial mammals. However,  $V_d/V_t$  diminishes with increasing  $V_t$  in humans and dogs (Bouhys, 1964), a pertinent observation in view of the relatively large  $V_t$  in the divers.

Fluctuations in arterial  $P_{O_2}$  and  $P_{CO_2}$  with respiration have been predicted in man and terrestrial animals (Otis, 1964; Suwa and Bendizen, 1972) and diving animals (Irving et al., 1941). Those fluctuations are influenced by: 1) the relative sizes of the tidal and resting lung volumes; 2) the relationship between resting lung volume and metabolic rate; 3) the relationship

between the fluctuating pulmonary blood flow and the fluctuating alveolar gas composition (Otis, 1964); and 4) the solubility of respiratory gases in pulmonary tissue. The greatest differences we observed were  $\Delta P_{O_2} = 36$  mm Hg and  $\Delta P_{CO_2} = 16$  mm Hg (Figure 8): These considerable excursions follow from the ratio of resting lung volume to tidal volume, which in the whale is about 2 and in man about 5; the ratio of resting lung volume to metabolic rate, which in the whale is about 20 and in man is about 10; and the very large difference between human and whale respiratory rates. Taken together, these relationships suggest that apneustic breathing in the whale is just as it seems: each breath interrupts a respiratory pause which actually represents a period of breathholding, during which appropriate changes occur in arterial blood gas tensions. Although tempting, approaches toward cardiac output computation are hampered by ignorance of the composition of mixed venous blood. Calculations of the "mean" alveolar gas or arterial blood composition are similarly hampered, and by imprecision in the sample collection timing as well.

## CONCLUSIONS

1. These two gray whale calves have provided the first opportunity for the collection of physiologic data from living baleen whales. The growth-rate in one of them was such that she became the world's largest captive animal.

2. Comparison of their size with that of whales in nature, and of their growthrate with one another and with other animals, strongly suggests that their size and growthrate were normal.

3. We observed increases in respiratory function and metabolism during growth similar to the increases in terrestrial mammals. In particular; relative increases in body weight; and of lung volume, minute ventilation, and metabolic rate as functions of body weight, proceeded in approxi-

mate parallel to the relative increases observed in man.

4. Interspecies comparisons of absolute lung volume and metabolic rate can also be based on body weight. Where the gray whale calves differed from correlations drawn between mammals including those at the extremes of body size, the departure could be explained by the whales' immaturity.

5. One of the whales entered a rapid growth phase, during which it gained approximately 1,000 kg/mo. Its gross efficiency for growth, calculated from the amount it ate and weighed, diminished from about 10 percent at a body weight of about 3,000 kg to about 7 percent at a body weight of 6,350 kg.

6. The relationships between tidal volume, resting lung volume, and wasted ventilation are similar in the gray whale calf to these in other diving mammals: although those relationships are different from the ones in terrestrial animals, they follow from the apneustic respiratory pattern (of infrequent but very large breaths interrupting long periods of breathholding at high lung volume).

7. The apneustic pattern of breathing also results in respiratory excursions in arterial oxygen and carbon dioxide tensions much larger than those predicted in terrestrial mammals.

## ACKNOWLEDGMENTS

Both whales were kept in pools at Sea World, Inc., an oceanarium in San Diego, Calif. The staff and administration extended to investigators courtesies and facilities both large and small, ranging from hot showers and coffee to underwriting the expeditions and the subsequent upkeep of the whales; and thereby made these studies both possible and enjoyable. In particular, Bud Donahoo and Sue Bailey provided Gigi II and her investigators with understanding and with expert assistance. We acknowledge with thanks the support of Robert Peterson and the crew of the *Falcon* involved in the capture,

transport, and maintenance of Gigi I. We are also grateful for the considerable assistance of Jack Schultz, Ken Hamai, James Wright, Brian D' Aoust, and Morgan Wells. Finally, we are grateful to the two Gigis, for they, by patiently enduring our several insults, made possible observations new to the largest and least accessible sub-order of living mammals.

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MFR PAPER 1046

## Ballistocardiography as a Technique for Comparative Physiology

N. TY SMITH and ERIC A. WAHRENBROCK

### ABSTRACT

*The ultra low-frequency ballistocardiogram was recorded on a young California gray whale. The tracing is remarkably similar to those obtained from man and mouse, both in amplitude and in form. The IJ amplitudes for mouse, man, and whale were 2.6, 4.3, and 4.6 cm/sec<sup>2</sup>. We conclude that greater differences are caused by poor recording technique or by disease than by species differences. The major interspecies differences were seen in the timing of cardiac events, such as prejection or ejection time. These differences could be caused by differences in heart size.*

The ballistocardiograph (Bcg) is a device for evaluating the mechanical function of the heart. It has been recorded in an incredible array of animals, ranging from egg embryos to cattle. One of the more interesting facts to arise from these recordings is that the tracings are remarkably similar among species, particularly mammals. This similarity holds both in form and in amplitude. It was therefore an excellent opportunity to

extend these observations to Gigi, an animal with an entirely different mass and configuration from other mammals previously used.

The Bcg records the movements of the body caused by movements of blood in the body. First recorded in 1887, the Bcg has undergone a series of ups and downs in its attempts to become a useful tool for measuring cardiovascular function noninvasively. Not until the 1950's when physicists and engineers entered the field, did the Bcg finally re-emerge as an accurate, relatively simple technique.

Essentially, the Bcg works on the principle that an attempted shift in the center of mass of a floating body is compensated for by a movement of the body in the opposite direction, so that the center of mass remains constant in

relation to a fixed point. Thus, if blood moves in one direction after ejection by the left ventricle, the body will move in the opposite direction. These movements are quite small, but the reader has certainly noticed a slight bodily movement as he lies quietly on a bed or a slight movement of the pointer on a weighing scale, each movement synchronous with the heart beat. This minute body movement can be recorded as displacement, velocity, or acceleration. Figure 1 shows examples of normal tracings in man. The important fact to note is that the major components of the Bcg occur during ejection of blood, particularly during the early portion.

### METHODS

When the physical scientists entered the field, they laid down certain standards for recording the Bcg, standards which were to convert ballistocardiography from a haphazard technique to a precise one. The first requirement is that a very light bed is necessary, in contrast to the heavy ones formerly used. A ratio of 10:1 for subject:bed is minimal. Second, coupling, or binding, of subject to bed must be as tight as possible. Third, coupling to ground must be minimal, so that ambient vibrations can be attenuated. The Bcg is an extremely sensitive instrument. Peak displacement is about 100 $\mu$ , peak acceleration, a few millig's, g being the acceleration of gravity. With older instruments, vibrations from a truck outside the building were able to destroy a bal-

**N. Ty Smith is an Associate Professor of Anesthesia at the University of California at San Diego, Veterans Administration Hospital, San Diego, CA 92161, and Eric A. Wahrenbrock is an Assistant Professor of Anesthesia at the University of California, San Diego.**